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Morphological variation in the Brazilian Radiated Swamp Turtle *Acanthochelys radiolata* (Mikan, 1820) (Testudines: Chelidae)

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Abstract

The freshwater turtle *Acanthochelys radiolata* (Mikan, 1820) is endemic to the Atlantic Forest domain in Brazil and few studies have been done on the morphology, geographic variation and taxonomy of this species. In this paper we record the morphological variation, as well as sexual dimorphism and ontogenetic changes in *A. radiolata* throughout its distribution range. We analyzed 118 morphological characters from 41 specimens, both quantitative and qualitative, and performed statistical analyses to evaluate size and shape variation within our sample. Morphological analysis revealed that *A. radiolata* is a polymorphic species, especially regarding color and shape. Two color patterns were recognized for the carapace and three for the plastron. Diagnostic characteristics of the species, such as the rounded tubercles on the neck and the shallow dorsal sulcus between the 2nd and 4th vertebral scutes, varied considerably. *Acanthochelys radiolata* also showed a high level of ontogenetic variation characterized by a change on the color pattern of plastron and limbs starting from the 4th month of life. Sexual size dimorphism was observed for the first time on nine morphometric variables and females showed larger sizes than males. Based on these results we conclude that *A. radiolata* represents one single polymorphic species distributed in the lowlands of the Brazilian Atlantic Forest from the state of Alagoas to the state of Rio de Janeiro and the south of Minas Gerais state.

Key words: geographic distribution, morphology, taxonomy, turtles

Resumo

A tartaruga de água doce *Acanthochelys radiolata* (Mikan, 1820) é endêmica da Mata Atlântica brasileira porém poucos estudos foram realizados sobre a morfologia, variação geográfica e taxonomia desta espécie. Neste estudo nós documentamos a variação morfológica, ontogenética e dimorfismo sexual de *A. radiolata*. Nós analisamos 118 caracteres, quantitativos e qualitativos, em 41 espécimes e executamos análises estatísticas para avaliar a variação de forma e tamanho dentro da amostra. A análise morfológica revelou que *A. radiolata* é uma espécie polimórfica, principalmente em relação a caracteres de forma e coloração. Dois padrões de coloração foram reconhecidos para a carapaça e três para o plastrão. Características diagnósticas da espécie, como os tubérculos arredondados no pescoço e o sulco longitudinal entre o segundo e quarto escudos vertebrais, variaram consideravelmente. *Acanthochelys radiolata* apresentou um alto grau de variação ontogenética, principalmente a partir do quarto mês de vida quando há uma mudança na coloração do plastrão e dos membros. Dimorfismo sexual de tamanho foi observado pela primeira vez em nove variáveis morfométricas e as fêmeas apresentaram maiores tamanhos que os machos. Baseado nestes resultados concluímos que *A. radiolata* representa uma única espécie polimórfica distribuída ao longo da baixada litorânea da Mata Atlântica brasileira desde o estado de Alagoas até o Rio de Janeiro e também no sul de Minas Gerais.

Palavras chave: Distribuição geográfica; morfologia; tartarugas; taxonomia

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Introduction

The Brazilian radiated swamp turtle *Acanthochelys radiolata* is restricted to the Brazilian Atlantic Forest domain (Souza 2004), ranging from northeastern Brazil, near the mouth of the São Francisco River in Alagoas state, south to the states of Minas Gerais, Rio de Janeiro, and São Paulo (Rhodin *et al.* 1984a; Iverson 1992; Fritz & Havaš 2007; TTWG 2011; 2014).

Rhodin *et al.* (1984a) mentioned the presence of a small population in the Culuene River, municipality of Jacaré, Mato Grosso state, western Brazil. Although only two specimens are known from this population, these authors state this configures a case of discontinuous geographic distribution since no other specimen was found between this population and those from the Atlantic coast.

Several studies are available for the other three species of the genus *Acanthochelys*, focusing on behavior, locomotion, feeding, and other aspects on ecology (Rhodin *et al.* 2009; Brasil *et al.* 2011; Neto *et al.* 2011; Vinke *et al.* 2011). However, biological data on *A. radiolata* is still scarce (Souza 2004), with the exception of the studies of Molina (1998) and Mocelin *et al.* (2008) that dealt with the reproduction of this turtle in captivity (Mocelin *et al.* 2008 also mentioned one nest found in nature).

There are also few recent studies on the taxonomy, systematics or even morphology of *A. radiolata* (Huebinger *et al.* 2013), hindering the definition of its conservation status (classified as "data deficient" by TFTSG Draft 2011 *in* TTWG 2014) due to lack of information about its geographic distribution, population biology and behavior (Ernst & Barbour 1989; Bonin *et al.* 2006).

In this paper, we discuss the morphological variability of *A. radiolata* based on the analysis of morphological and morphometric characters. Moreover, we evaluate the taxonomic status of the species in order to provide subsidies for the conservation of this taxon.

Material and methods

Material. We examined 41 specimens (all preserved in alcohol) of *A. radiolata* representing the entire known geographic distribution range of the species (Appendix 1). Specimens are housed in the following institutions: Museu Nacional, Rio de Janeiro, Brazil (MNRJ), Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil (MZUSP), and Museu de Zoologia da Universidade Estadual de Campinas, Campinas, Brazil (ZUEC). We also analyzed photographs of the holotype (NMW 23390) deposited in the Naturhistorisches Museum Wien, Austria.

Other specimens of *A. spixii*, *A. macrocephala* and *A. pallidipectoris* from the herpetological collections of MZUSP, MNRJ and Museu de Zoologia da Universidade Federal de Viçosa (MZUFV; Appendix 1) were also analyzed for comparative purposes.

Morphological analysis. We employed a total of 118 characters on external morphology of the shell, head and feet to evaluate intraspecific variation, from which 28 were morphometric characters, 12 quantitative meristic data, 66 qualitative morphological characters, and 12 related to color pattern (Supporting Information—Appendix S1). These characters were selected from descriptions of *A. radiolata* and other turtle species (Mikan 1820; Luederwalt 1926; Ernst 1983; Ernst & Barbour 1989; Lovich & Ernst 1989; McCord *et al.* 2001; Bonin *et al.* 2006; Dustman 2013), as well as from personal observations (new characters are listed in Appendix S1). All measurements were taken on the right side of the body using a vernier caliper to the nearest 0.02 mm (Supporting Information–Fig. S1). Length and width measures were taken along the anteroposterior axis of each specimen.

Meristic quantitative data (*e.g.*, number of scales, barbels and scutes) were taken from both sides of the body, considering the highest count when counting was different on each side. Here we propose some new quantitative characters for the taxonomy of *A. radiolata* rarely used for this purpose (Appendix S1).

Color pattern and morphological qualitative data here analyzed correspond to main characteristics of the shell and head, as well as some minor morphological structures (*e.g.*, snout, tympanum, tubercles of the neck and tail, and limb scales).

We classified specimens as adults, subadults or juveniles based on morphological characteristics. The sex of adults was determined by the presence of plastral concavity and the precloacal length (modified from Bujes *et al.* 2011). The present sample was constituted by 27 adults (11 males and 16 females), six juveniles and eight

subadults (animals without secondary sexual characteristics but almost with the carapace size of an adult).

Statistical analysis. To ascertain sexual size dimorphism in *A. radiolata* we performed a *Student's t*-test for independent groups using 18 morphometric characters (Fig. S1). We tested the sexual identification method of Dustman (2013) for some adult specimens, comparing the ratios of precloacal length (PCL) and plastral posterior lobe length (PLL) between males (concave plastron) and females (flat plastron). Assumptions of normality and homoscedasticity were evaluated through Kolmogorov-Smirnov and Levene's tests, respectively (Zar 1999).

In order to understand the size and shape variation between specimens from different geographic areas, a Principal Component Analysis (PCA; Sneath & Sokal 1974) was performed using nine morphometric variables (HL—head length, HW—head width, CML—carapace median length, CWA—carapace width at anterior margin, CWP—carapace width at posterior margin, CH—carapace heigth, 4VL—4th vertebral scute maximum length, PML—plastron median length, PWB—plastron maximum width including/at the bridge) and only adult specimens.

All specimens were allocated into five populations (Fluminense, Paraíba do Sul, Northeastern Mata Atlântica, Coastal drainages, Xingu; Fig. 1) according to the limits of the freshwater ecoregions of the world (Abell *et al.* 2008). The PCA was performed independently for males and females to discard biases caused by sexual size dimorphism. We treated the missing data in the matrix by replacing them with the average of the given variable ("mean substitution" option). All statistical analyses were performed on the software STATISTICA 7.0 (Statsoft 2004).

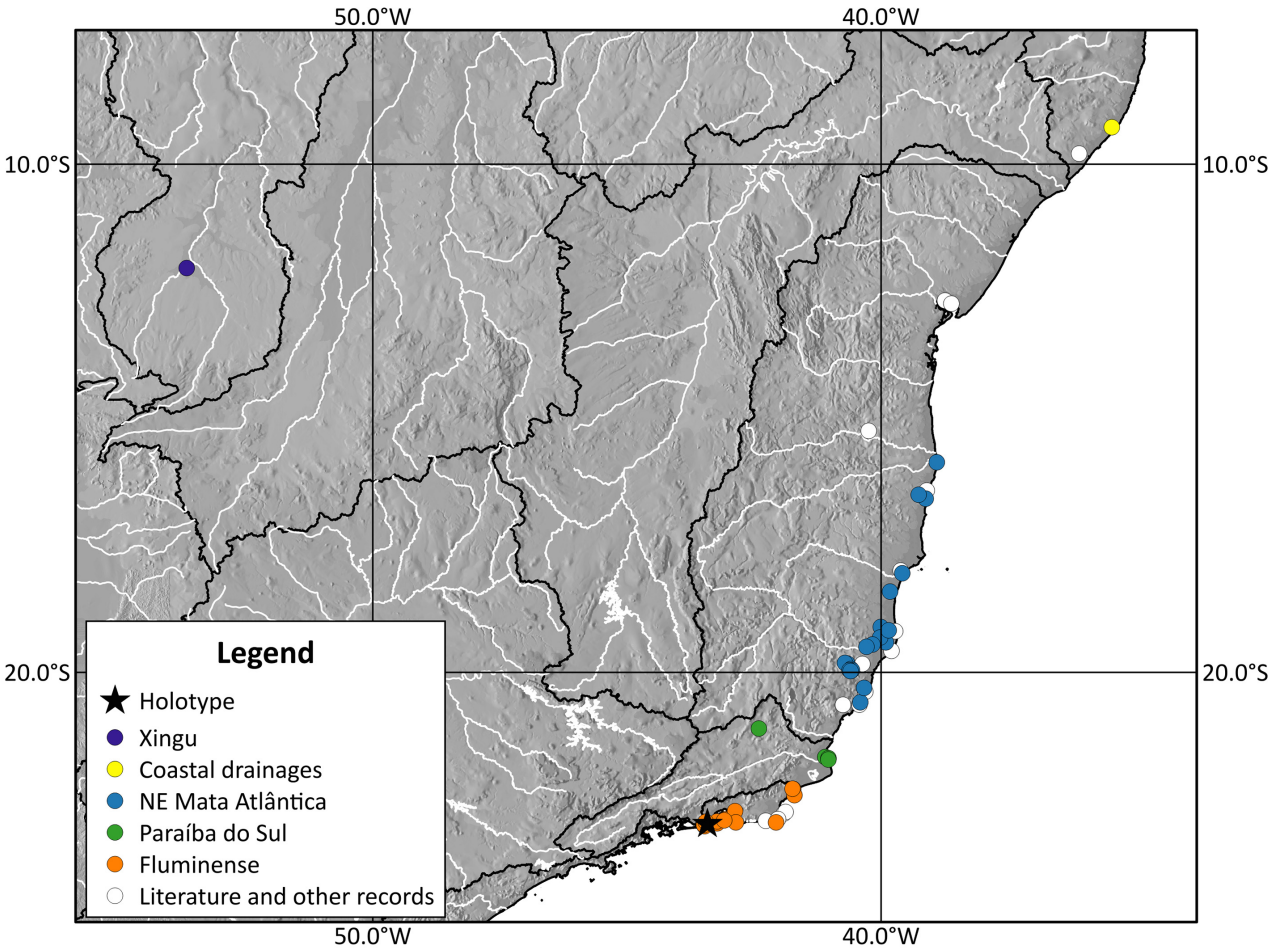

FIGURE 1. Geographic distribution of *Acanthochelys radiolata* based on the sampled specimens and literature analyzed. Specimens are assigned to populations according to freshwater ecoregions (Abell *et al.* 2008).

Results

Statistical analysis. Ten variables showed significant results ($p < 0.05$) for sexual size dimorphism (Table 3), with females always reaching larger sizes. The variables carapace width at anterior rim (CWA) and plastron median length (PML) showed no homoscedasticity and therefore were discarded from this analysis.

The sexual identification method using the rate PCL/PLL also revealed significant differences between males and females ($p = 0.043$; Table 1), females showing smaller values due to the longer precloacal length in males. Little overlapping was observed between females ($0.08 < x < 0.36$) and males ($0.26 < x < 0.46$) with respect to this ratio in the sample here analyzed.

TABLE 1. Descriptive statistics by sex and *t Student* test results of the morphometric variables of *Acanthochelys radiolata*. Measurements (in mm) are reported as minimum–maximum, mean ± SD. For abbreviations see Appendix 2.

CHARACTER	FEMALE	MALE	T	p
HL	34.60–42.70 (38.29 ± 2.27)	33.4–40.7 (36.83 ± 2.41)	1.53	0.141
HW	26.38–33.70 (29.6 ± 2.17)	24.36–30.14 (27.27 ± 1.76)	2.86	0.009
IOW	4.26–6.72 (5.74 ± 0.72)	4.56–6.26 (5.47 ± 0.59)	1.01	0.322
CL	145.5–195.1 (173.41 ± 14.67)	152.78–183.9 (162.81 ± 8.5)	2.15	0.041
CML	144–193.16 (172.04 ± 14.57)	151.14–182.16 (161.11 ± 8.38)	2.24	0.034
CW	104.8–140.56 (120.15 ± 9.71)	104.94–128.56 (112.56 ± 7.3)	2.20	0.038
CWP	97.12–131.38 (114.38 ± 9.35)	96.42–125.02 (107.53 ± 7.92)	1.98	0.058
CH	54–77.2 (65.06 ± 7.79)	45.92–60.68 (53.11 ± 4.26)	4.21	0.0003
PL	138.24–178.24 (159.27 ± 12.63)	135.94–164.06 (146.02 ± 8.49)	3.03	0.006
PW	75.76–97.62 (86.27 ± 6.66)	71.52–85.14 (77.71 ± 4.69)	3.67	0.001
PWB	92.20–122.32 (105.3 ± 8.59)	89.4–106.8 (97.03 ± 6)	2.75	0.011
PLL	41.08–58.34 (49.67 ± 4.62)	40.18–46.7 (43.47 ± 2.78)	2.75	0.016
BL	48.14–76.92 (62.51 ± 9.65)	55.08–59.88 (57.17 ± 2.01)	1.07	0.305
BW	11–21.26 (17.06 ± 2.96)	14.6–17.06 (16.04 ± 1.04)	0.66	0.523
PCL	4.06–18.86 (9.91 ± 4.34)	12.22–18.58 (14.39 ± 3.63)	-1.60	0.142
CVL	14.9–19.66 (17.62 ± 1.39)	10.86–20.66 (16.97 ± 2.76)	0.88	0.387
4VL	23.7–34 (29 ± 3.15)	24.1–33.48 (27.21 ± 2.47)	1.57	0.128
3PL	25.86–34 (30.47 ± 2.26)	25.42–30.56 (27.64 ± 1.51)	3.62	0.001
PCL/PLL	0.08–0.36 (0.20 ± 0.09)	0.26–0.46 (0.34 ± 0.11)	-2.31	0.043

The results of the PCA for females ($n = 16$) show that the first four principal components (PC) corresponded to 95.3% of the total variation of the sample. The projections of the scores of the principal components (Fig. 2) show a small segregation between the variation of the specimens from populations Northeastern Mata Atlântica and Fluminense for PC1. This segregation was mostly contributed by the variables CML (NE Mata Atlântica mean = 180.7 mm; Fluminense mean = 158.5; $p = 0.005$) and PML (NE Mata Atlântica mean = 155.7; Fluminense mean = 137.8; $p = 0.003$). Meanwhile, the projection of the scores of PC2, PC3 and PC4 expressed no segregation between ecorregions.

The first four principal components for male specimens corresponded to 94.27% of the total variation of the sample. Unlike females, no clear segregation between populations was found on the projection of the scores of PC1, PC2, PC3 and PC4.

Morphological variation. Here we present a general description of the morphological and color pattern variation of distinct regions of the body separately. The percentage of specimens analyzed that correspond to the variation of each character is shown in parenthesis.

Head (Fig. 3)—oval-shaped, larger posteriorly, flattened dorsally. Head always with scales positioned dorsally, laterally and ventrally (82.14%) or only dorsally and laterally (17.86%); except for the mesodorsal region frequently not with scales, but only with minor scratches (57.14%). Eyes positioned anterolaterally (53.57%) or

anterodorsally (35.71%). Snout short, somewhat inclined upward in lateral view (33.33%); snout flat (62.5%), pointed (31.25%) or straight (6.25%) in dorsal view. Upper jaw with no median notch; posterior end of upper jaw anterior (62.96%) or at the same level (37.04%) of the anterior region of the orbit. An excrescence of skin can be present at the posterior end of the mouth (71.43%). Barbels very short to medium.

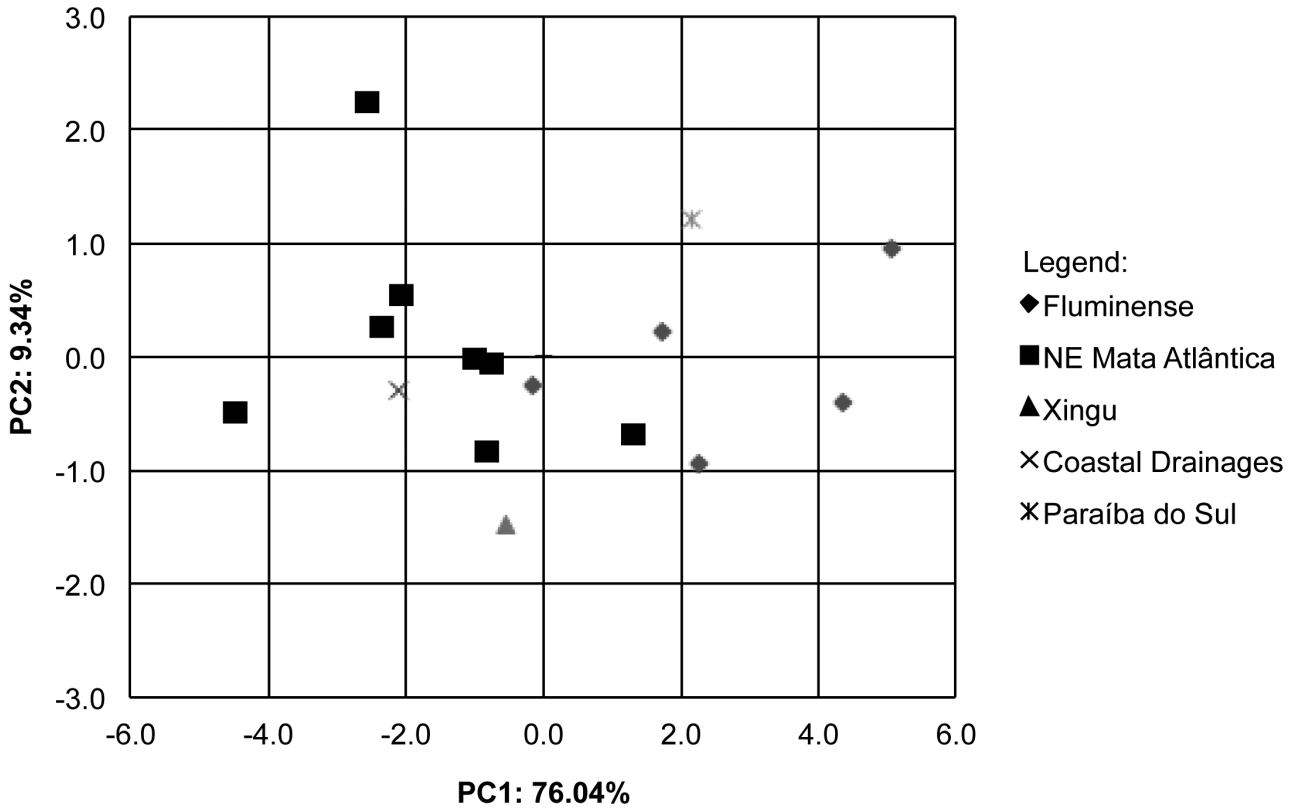

FIGURE 2. Projection of the scores of females of *A. radiolata* for PC1 and PC2. Symbols represent different ecoregions.

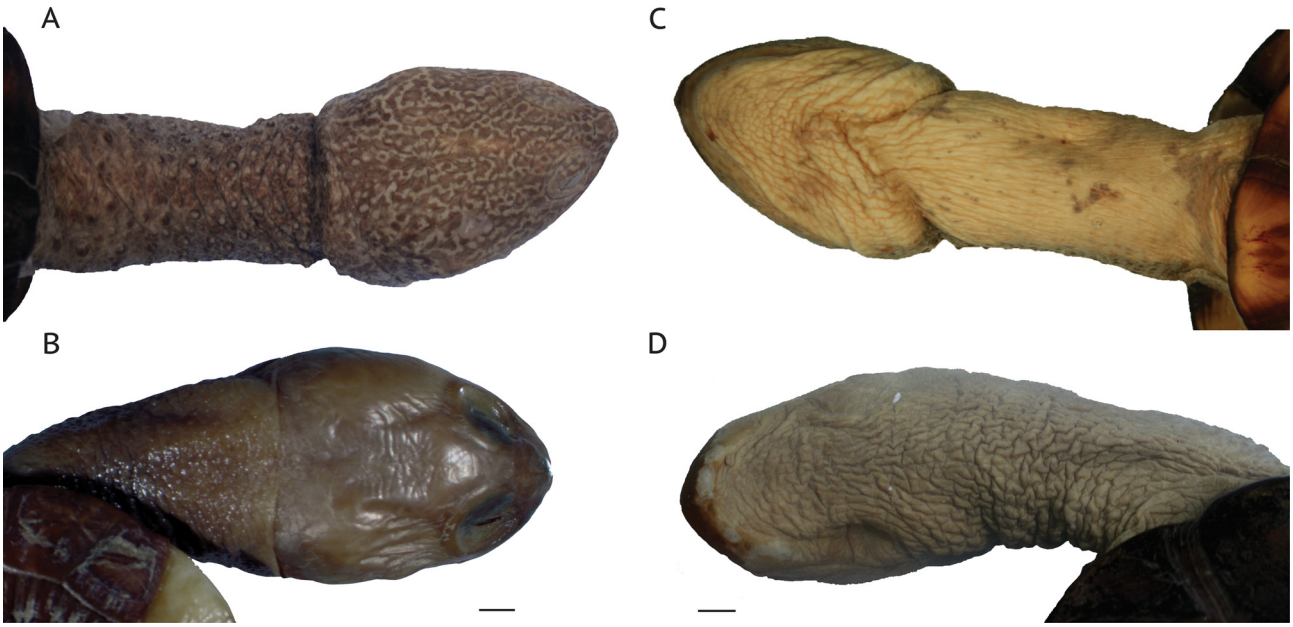

FIGURE 3. Variation in dorsal and ventral coloration of the head and neck. (A) Yellowish brown with light yellow lines (present in 80% of the specimens; MNRJ 7282). (B) Yellowish brown with uniform coloration (20%; MNRJ 1050). (C) Cream to yellow, with few small dark blotches (46.67%; MNRJ 7282). (D) Creamish brown, completely uniform coloration (13.64%; MNRJ 1055). Scale bar: 5 mm.

Color pattern. Dorsal ground color creamish (60%), yellowish brown (23.34%), or completely black (13.34%); usually with light yellow lines (80%) or with completely uniform coloration (20%). Ventral coloration usually cream to yellow (73.34%) or creamish brown (13.64%), often with a few small dark spots anteriorly (46.67%). Upper jaw with a reticulated pattern of brown with yellow lines (63.33%), yellow with brown lines or spots (20%), or completely brown (13.33%). Lower jaw yellow with dark lines or spots (40%), brown with yellow lines (20%), completely brown (23.33%) or cream (10%).

Neck (Fig. 3)—scales usually present (82.76%), positioned dorsally, laterally and ventrally. Dorsal tubercles always present with variable shape: rounded, pointed or oval; usually absent at posteriormost region of the neck (70.83%). Lateral tubercles always present, short or very short, with irregular shape. Ventral surface with no tubercles, but usually with longitudinal skinfolds (82.76%).

Color pattern. Dorsal coloration dark brown to black (65.63%), sometimes light brown (34.38%). Ventral coloration usually cream with small dark spots (50%), completely cream (18.75%) or brown (15.62%).

Carapace (Figs. 4 and 5)—frequently oval-shaped, larger posteriorly (65.63%) or elliptic (21.88%). Slightly convex dorsally (62.5%), with a median sulcus (51.61%) or completely flat (48.39%) between the 2th and 4th vertebral scutes (48.39%). Lateral margins always slightly upturned, forming shallow gutters usually between the 3th and 8th marginal scutes. Anterior margin frequently rounded (73.33%), sometimes straight between the 1st marginal scutes (26.67%). Maximum width of the carapace usually at the 7th marginal scute (54.84%) and maximum height usually at the level of the posterior region of the 3th vertebral scute (78.13%). Cervical scute usually longer than wide (90.47%), sometimes as long as wide (9.53%). Each carapacial scute frequently with growth annuli and radiating striations. Ventral surface of marginal scutes sometimes with growth annuli (63.63%), but frequently with no radiating striations (84.84%).

Color pattern. Reddish dark brown coloration with wide orange stripes and thin brown stripes over each scute, creating a radiating color pattern (50%). This pattern has some variations (Fig. 4): (**1**) reddish dark brown with brown blotches over each scute (17.64%); (**2**) reddish dark brown with thin brown stripes and yellow margin on each scute (11.76%); and (**3**) uniform reddish dark brown, with no stripes (11.76%). Other pattern variations are unpatterned black (17.68%) or black with white or gray radiating stripes (14.67%).

Plastron (Figs. 6 and 7)—anterior lobe always wider and longer than posterior lobe. Anterior margin rounded, usually not reaching (in length) the anterior margin of the carapace (81.25%). Posterior margin always with a notch between anal scutes, usually not reaching (in length) the posterior margin of the carapace (55.88%). Intergular scute always completely separating gular scutes but not the humerals (Fig. 6); longer than wide, anterior margin with a simple contact (71.87%) or overlapping anterior margin of gular scutes; median length of intergular scute shorter (39.39%), equal (36.36%) or longer (24.24%) than its distance to abdominal scutes. Pectoral scutes always two times or more wider than long; usually contacting axillary scute (when present), the 5th and 6th marginal scutes (48.48%), or only the 4th and 5th marginal (12.12%); pectoral-abdominal suture frequently in contact with 6th marginal scute. Abdominal scutes always wider than long; usually contacting inguinal scute (when present), and 6th and the 7th marginal scutes (84.84%). Plastral formula variable (Table 2): intergular > < femoral > abdominal > < humeral > < gular > < anal > < pectoral. All plastral scutes frequently with growth annuli (90.62%) and radiating striations (70.96%), which can be sometimes only softly marked over the scutes (52%) or clearly distinct (48%).
Color pattern. Background color yellow with thin brown streaks, creating a radiating pattern from lateral margin of each scute (67.64%). This pattern has some variations regarding the quantity of brown streaks (Fig. 6): (1) yellow background with a dark brown blotch along sutures of the scutes, due to the concentration of brown streaks (32.35%); (2) yellow background with few brown streaks (5.88%). Few specimens showed a totally black coloration with lateral yellow blotches (8.82%) and only one specimen (MNRJ 19822) presented an abnormal coloration: completely yellow with a dark blotch along the sutures, but no streaks.

Forelimbs (Fig. 8)—lateral surface covered with large scales arranged in a longitudinal line, increasing in size distally. Medial surface covered with scales of irregular shape, varying from very small to median sized scales. Interdigital webbing well developed, frequently posterior (71.42%) or at the same level of claw insertion (28.58%). Lateral surface skin coloration brown to black with scales of the same color (90.63%); scales with a yellow line at posterior rim (18.75%). Medial surface skin coloration yellow with scales darker, gray or black (18.75%); scales often with small dark spots (43.75%).

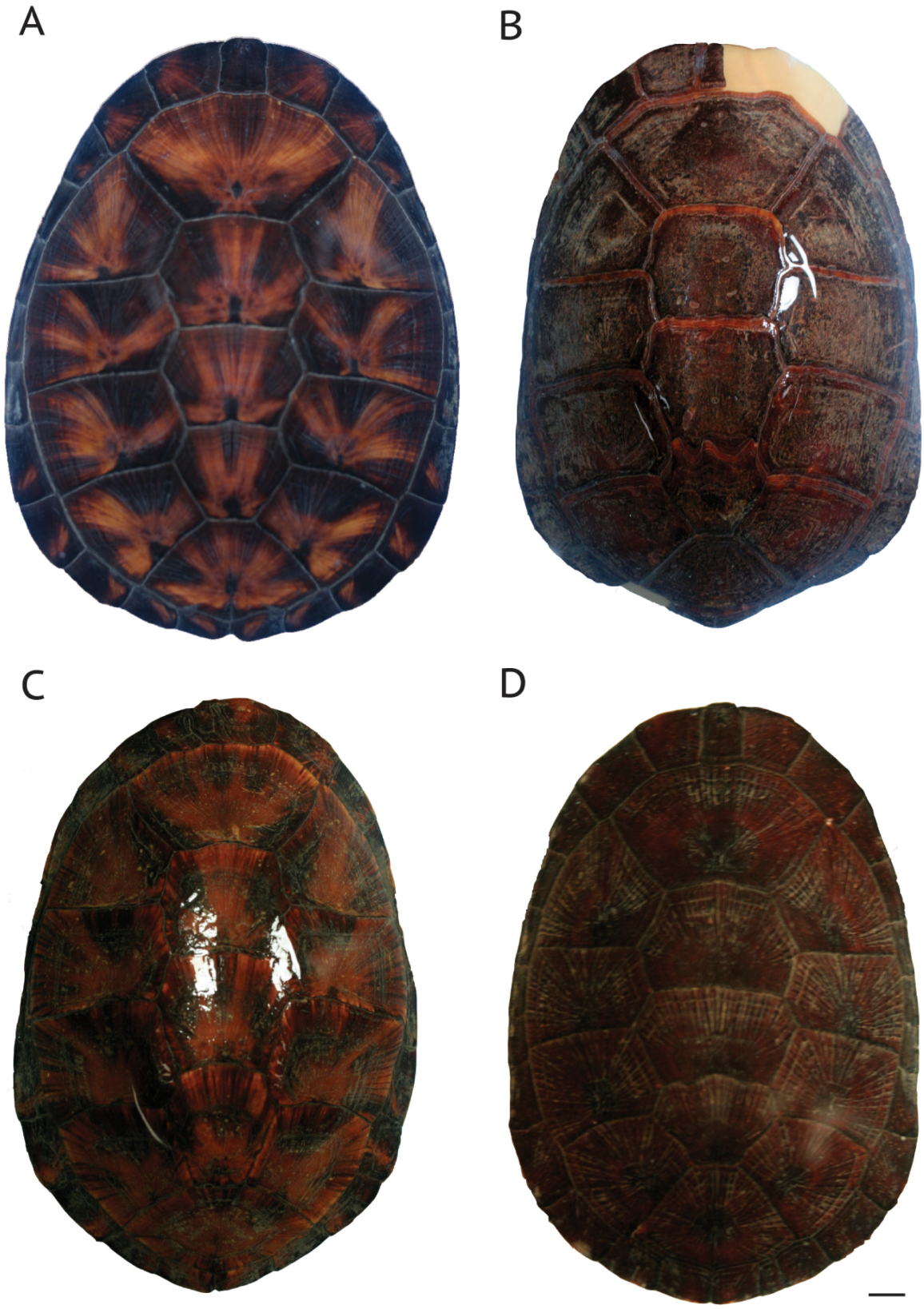

FIGURE 4. Variation in carapace coloration of *A. radiolata*—reddish dark brown coloration pattern. (**A**) Reddish dark brown with large orange radiating stripes and thin brown stripes over each scute (50%; MNRJ 7282). (**B**) Reddish dark brown with brown blotches over each scute (17.64%; MNRJ 1056). (**C**) Reddish dark brown with thin brown stripes and yellow margin on each scute (11.76%; MNRJ 2466). (**D**) Completely reddish dark brown, with no stripes (11.76%; MNRJ 3810). Scale bar: 10 mm.

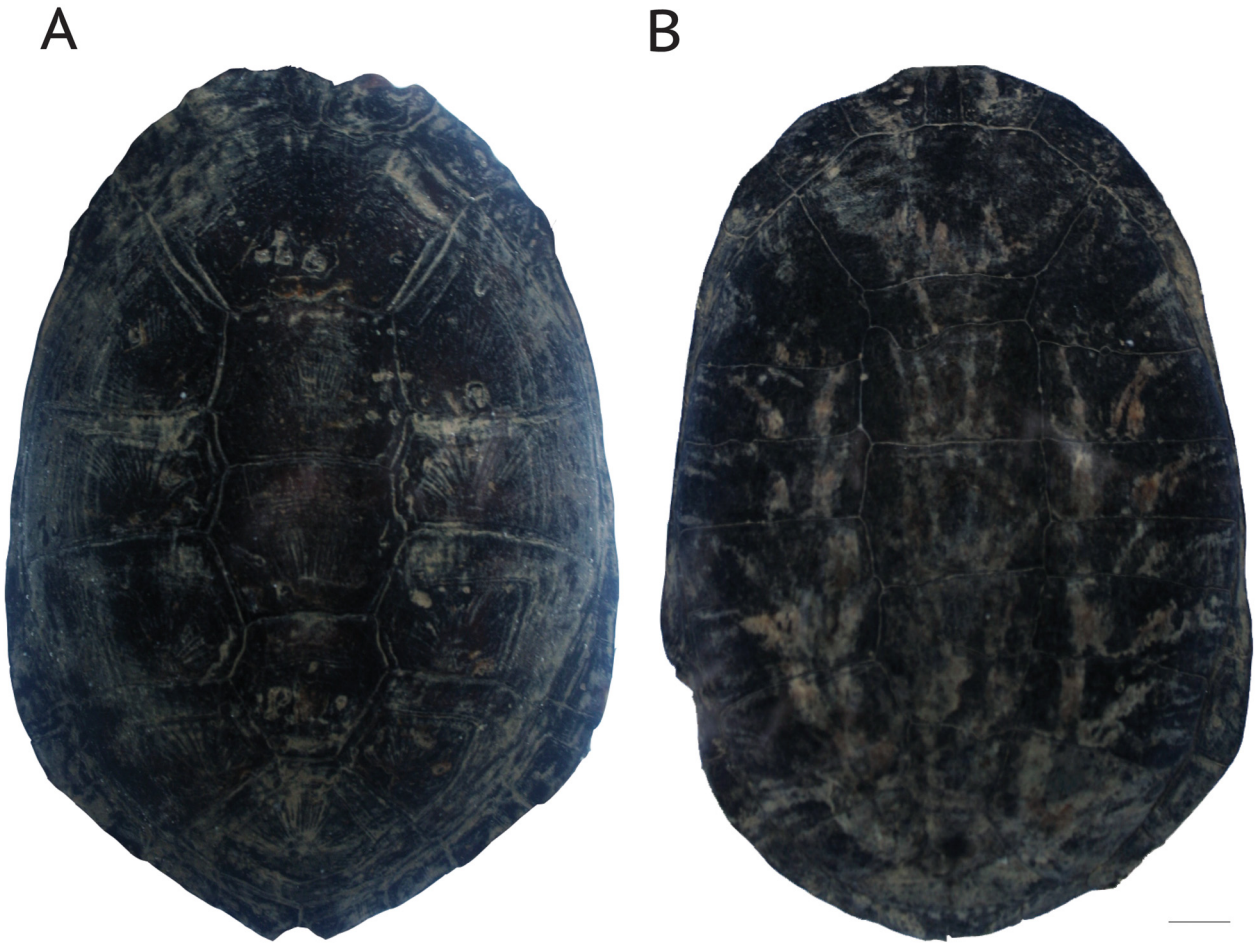

FIGURE 5. Variation in carapace coloration of *A. radiolata*—black coloration pattern. (A) Completely black (17.68%; MNRJ 20068). (B) Black with white or gray radiating stripes (14.67%; MNRJ 19822). Scale bar: 10 mm.

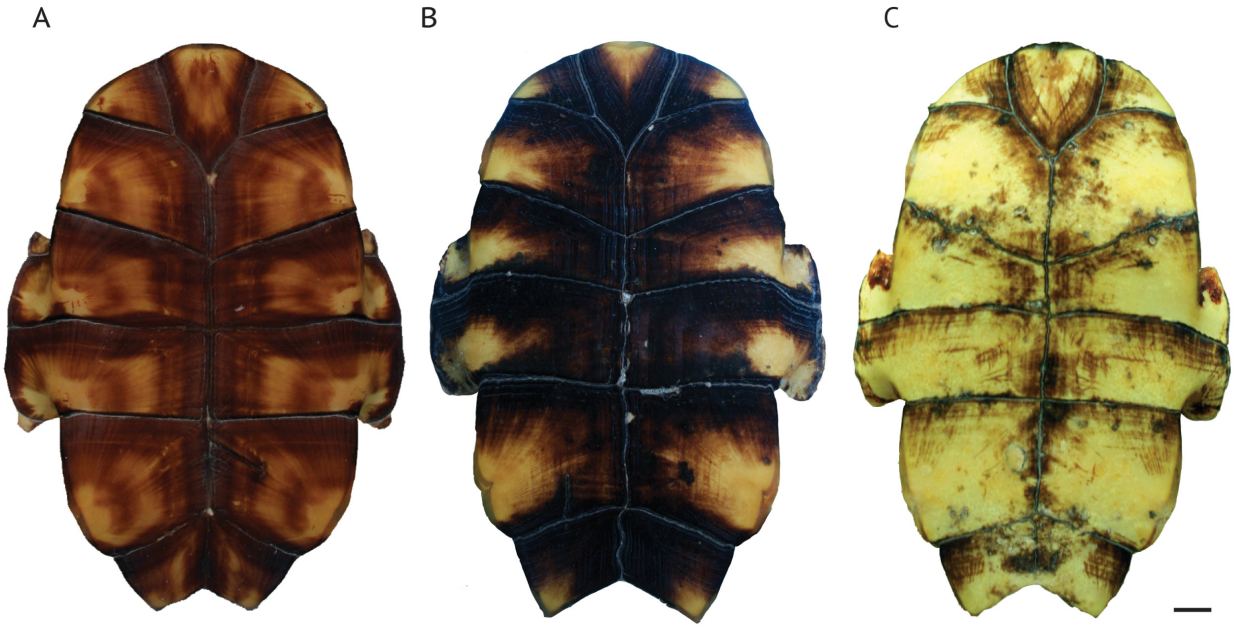

FIGURE 6. Variation in plastral coloration of *A. radiolata*—radiating color pattern. (A) Background coloration yellow with thin radiating brown streaks (MNRJ 7282). (B) Yellow background with a dark brown blotch along the sutures of the scutes, due to the high concentration of brown streaks (32.35%; MNRJ 7308); (2) Yellow background with few brown streaks (5.88%; MZUSP T-3035). Scale bar: 10 mm.

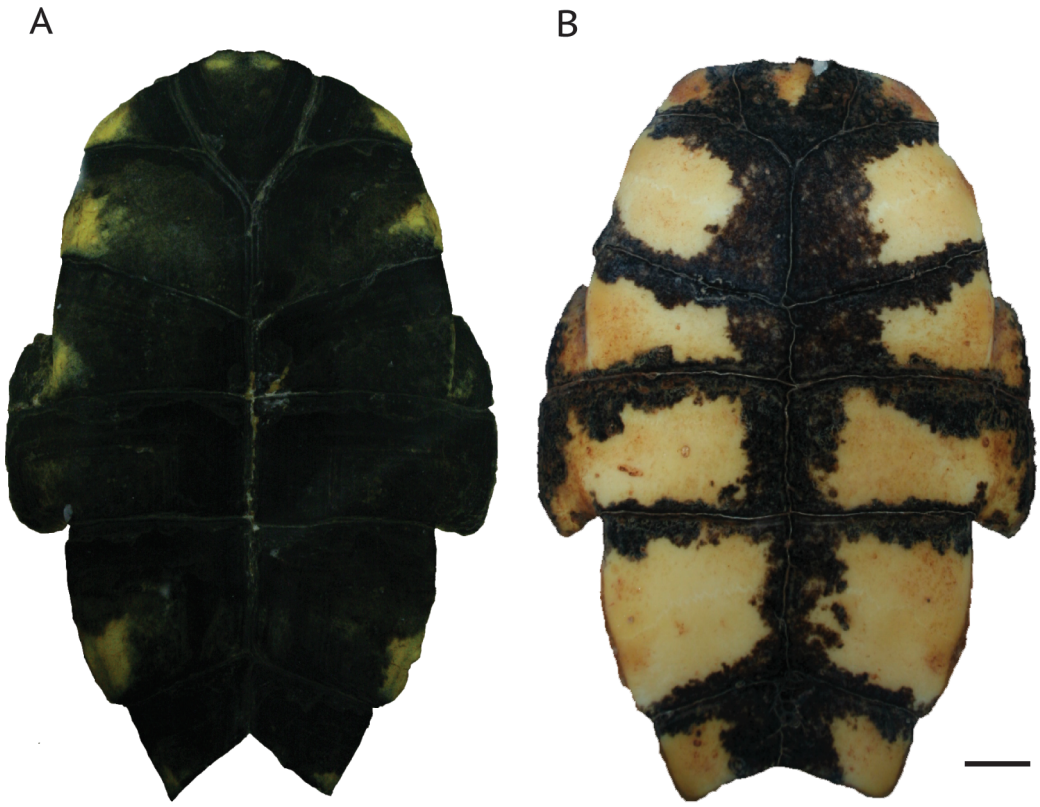

FIGURE 7. Variation in plastral coloration of *A. radiolata*—less frequent coloration patterns. (**A**) Black coloration with lateral yellow blotches (8.82%; MNRJ 19625). (**B**) Yellow background with a dark blotch along the suture of the scutes with no streaks (MNRJ 19822). Scale bar: 10 mm.

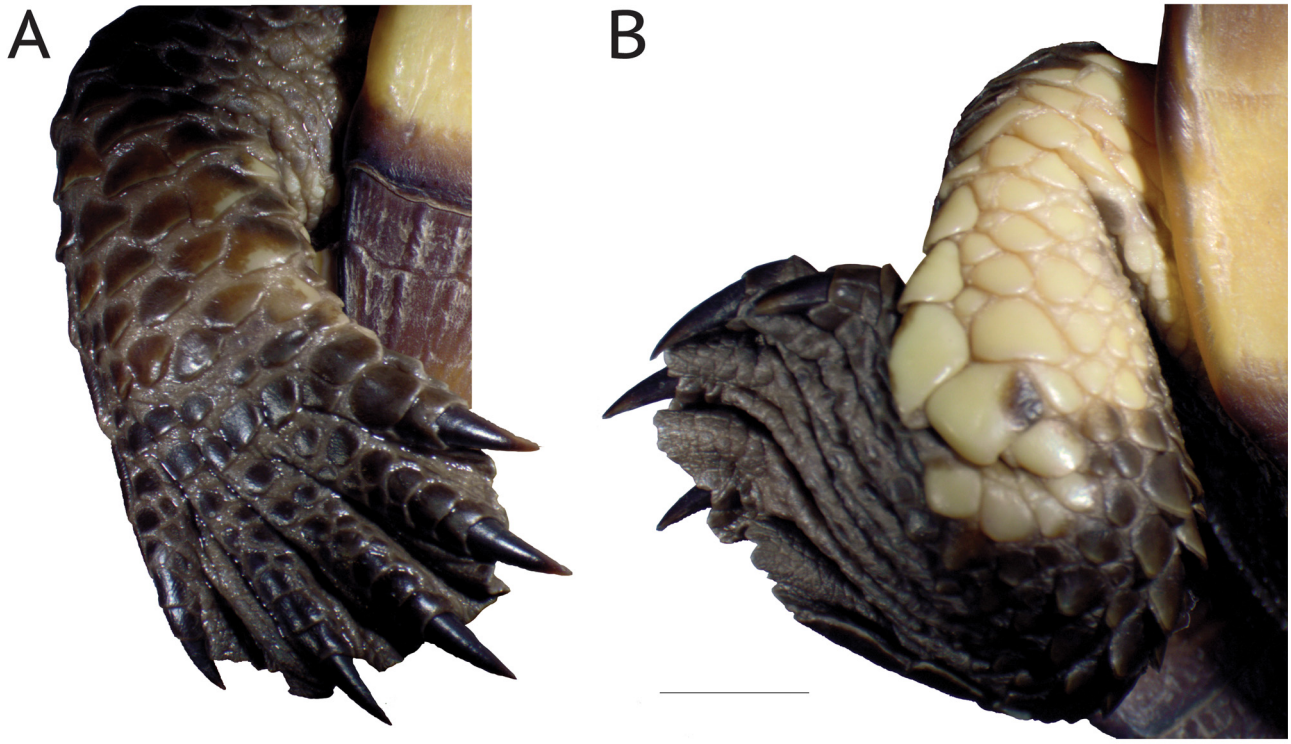

FIGURE 8. Variation in the coloration pattern of the limbs of *A. radiolata* (MNRJ 3810). (A) Forelimb, lateral surface brown and scales of the same color with a yellow line at posterior rim (18.75%); (B) Hindlimb, ventral surface completely yellow with scales of the same color (45.45%). Scale bar: 10 mm.

TABLE 2. Plastral formula variation in a sample of *Acanthochelys radiolata*.

Plastral formula	N	Males	Females	Juveniles/subadults
Interg > fem > abd > hum >gul > anal > pect	4	3	1	
Interg > fem > abd > gul > hum > anal > pect	3		1	2
Interg > fem > gul > abd > hum>anal > pect	3	1		2
Interg > anal > gul > fem > abd > pect > hum	1			1
Interg > fem > abd > anal > hum > gul > pect	1			1
Interg > fem > abd > gul > anal > hum > pect	1			1
Interg > fem > abd > hum > anal > pect > gul	1			1
Interg > fem > abd > hum > gul > pect > anal	1		1	
Interg > fem > anal > abd > gul > hum > pect	1			1
Interg > fem > hum > abd > anal > gul > pect	1		1	
Interg > fem > hum > anal > gul > abd > pect	1			1
Interg > gul > fem > abd > hum > anal > pect	1			1
Fem > abd > interg > hum > anal > gul > pect	1		1	
Fem > interg > abd > hum > anal > gul > pect	1		1	
Fem > interg > hum > abd > gul > anal > pect	1		1	
Fem > interg > hum > abd > gul > pect > anal	1		1	

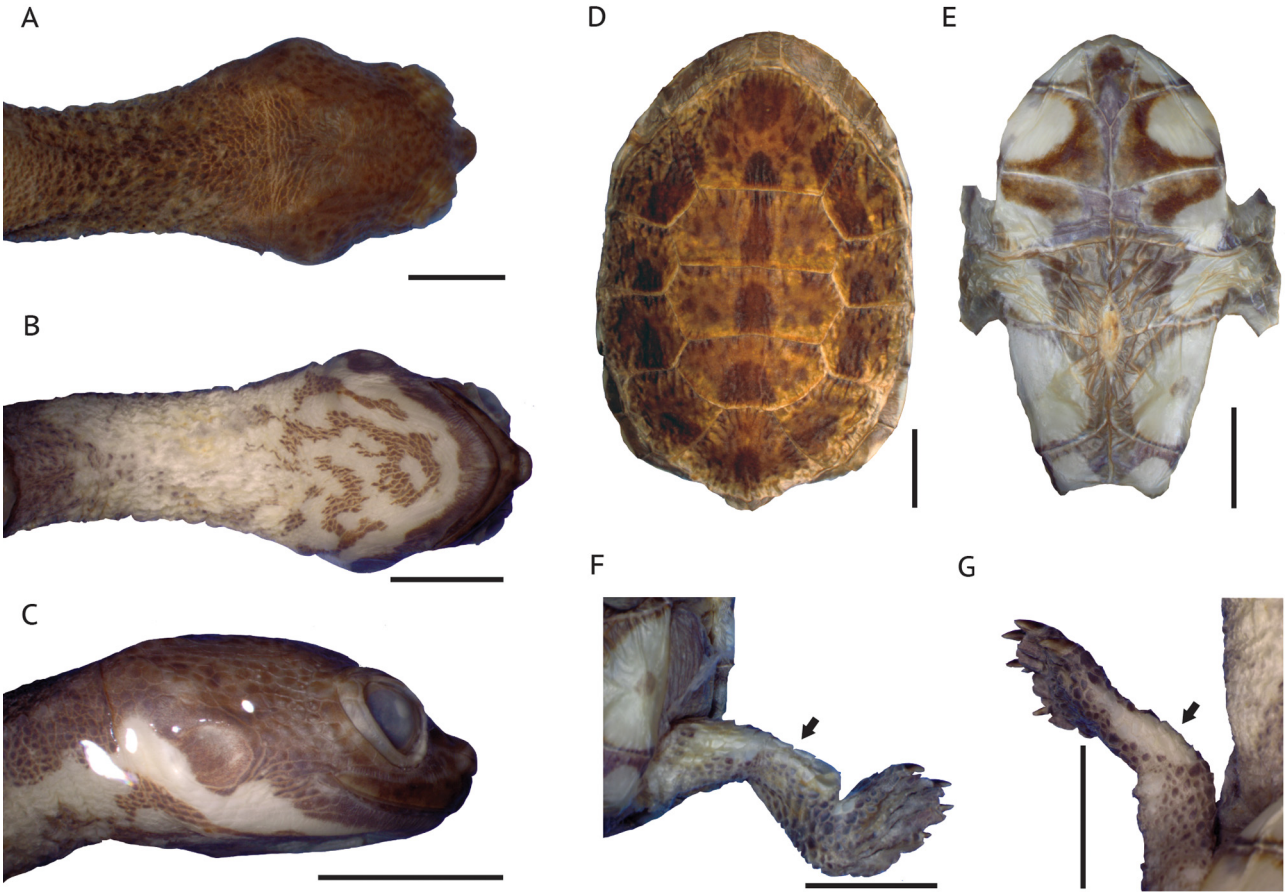

FIGURE 9. Coloration pattern and morphology of a juvenile of *A. radiolata* (MNRJ 7280). (A, B, C) dorsal, ventral and lateral view of head and neck, respectively; (D) carapace; (E) plastron; (F, G) hindlimb and forelimb. Note the size of the yellow blotch in the medial surface of each limb (arrow). Scale bar: 5 mm.

Hindlimbs (Fig. 8)—lateral surface covered with irregular shaped scales of variable sizes. Medial surface with large tibial scales arranged in longitudinal line, increasing in size distally. Five digits covered with irregular shaped scales; digit V frequently reduced with no claw, except for one specimen (MZUSP T-0062) that had a small pointed claw. Interdigital webbing well developed, frequently posterior to insertion of claws (80.64%). Thighs with posterior tubercles of variable shape, close to the tail: pointed, blunt, rounded or oval shape; largest tubercles arranged in a transversal line and frequently one of the tubercles is larger than the others (81.48%).

Color pattern. Lateral surface skin coloration brown to black (90.90%) with scales of the same color; scales with a yellow line at posterior rim or small yellow spots (13.34%). Medial surface skin coloration yellow; scales completely yellow (45.45%), yellow with small dark spots (33.33%), or completely grayish (12.12%).

Juvenile morphology (Fig. 9)—juveniles differed morphologically from adults, especially in color pattern and the morphology of some body regions. Dorsal coloration of head as in adults: dark with light yellow lines (60%). Ventral coloration of head yellow with longitudinal brown lines reaching the neck (60%). Upper and lower jaws uniformly brown.

Carapace coloration light brown with darker posterior blotch on each vertebral and pleural scute (60%) or each scute with dark brown sulcus (20%). Hatchlings and very small specimens (CL < 38 mm) without radiating striations on the scutes, showing irregular unordered striations, and with 2nd to 4th vertebral scutes much larger than long. Juveniles with CL > 45 mm showed irregular striations although a radiating pattern is visible. Cervical scute as long as wide. Notch between 12th marginal scutes absent or greatly reduced.

Plastron coloration light yellow with a gray to brown central blotch, following the median seams, with no streaks or mottling (60%). Intergular scute separates gular scutes but not the humerals. Both axillary and inguinal scutes present.

In small specimens (CL < 45 mm), forelimb and hindlimb coloration completely dark brown with a light yellow blotch on medial surface. However, in juveniles with a CL > 74 mm only the lateral surfaces are dark brown while the medial surfaces are almost completely light yellow.

Quantitative morphology (Table 3)—all characters analyzed here showed low variability (as stated by low SD values), which show that this type of data is consistently independent of life stages or sex.

TABLE 3. Descriptive statistics of the quantitative morphological characters for *Acanthochelys radiolata*. Number of specimens (N); Variation scale (MIN–MAX); Standard deviation (SD).

CHARACTER	N	**MIN–MAX MEAN ± SD**	COMMON STATE (%)
Number of post-orbital scales	29	2–6 (4.62 ± 0.82)	4 (38%)
Number of post-nasal scales	28	0–3 (1.14 ± 0.52)	1 (82%)
Number of tympanum-orbit scales	30	3–5 (4.33 ± 0.61)	4 (53%)
Number of barbels	30	1–2 (1.93 ± 0.25)	2 (93%)
Number of marginal scutes	36	12–14 (12.17 ± 0.38)	12 (83%)
Number of forelimb lateral scales (in line)	31	6–10 (7.58 ± 0.92)	7 (48%)
Number of forelimb flap lateral scales	31	4–8 (6.16 ± 1.13)	6 (32%)
Number of forelimb fist scales in line	31	4–6 (4.94 ± 0.73)	5 (48%)
Number of hindlimb lateral scales (in line)	33	5–8 (6.24 ± 0.87)	6 (39%)
Number of hindlimb flap lateral scales	33	4–7 (5.42 ± 0.83)	5 (42%)
Number of post-hindlimb tubercles (in transversal line)	30	0–8 (4.5 ± 1.38)	4 (40%)
Number of dorsal scales on digit I of hindlimb	30	3–5 (3.77 ± 0.5)	4 (73%)

Discussion

Morphological variation. This study provides a detailed description of the morphological variation within *Acanthochelys radiolata*, which has only been treated rarely in the past (Mikan 1820; Duméril & Bibron 1835;

Ernst & Barbour 1989). For the first time a large number of quantitative characters were analyzed in this species (28 morphometric and 12 meristic characters) and many of them were not examined previously in the literature (see Appendix S1).

Morphometric data revealed that *A. radiolata* is a small to medium-sized turtle and is the second largest species of the genus, surpassed in size only by *A. macrocephala,* which can reach a CL of up to 295 mm (Rhodin *et al.* 2009). The other two species, *A. spixii* and *A. pallidipectoris*, have a maximum CL around 170 and 180 mm, respectively (Ernst & Barbour 1989; Vinke *et al.* 2011).

The meristic quantitative characters analyzed, which are rarely used for taxonomic purposes in turtles, including the Chelidae (Ernst 1983), here varied little compared to other types of data. Some new characters such as the "number of forelimb fist scales", the "number of hindlimb lateral scales" and the "number of hindlimb flap lateral scales" showed low variability even when juveniles and adults were analyzed together (see Table 1). The absence of ontogenetic variation and sexual biases in these characters indicates that these are putative new diagnostic characters of the species. Unfortunately, only few specimens of the other species of *Acanthochelys* were available to us and we could not confirm this hypothesis. A greater sample is needed to understand and compare the variation of meristic quantitative data within *Acanthochelys* and other species of Chelidae.

Part of the morphological data obtained here was consistent with previous descriptions in the literature (Mikan 1820; Gray 1844; Boulenger 1889; Ernst & Barbour 1989; Bonin *et al.* 2006), while others were not previously reported and are discussed below.

Head is covered by irregular dorsal scales as described by Boulenger (1889), but the mesodorsal region of the head is smooth (has no scales), occasionally showing minor scratches (57.14%). The barbels, as in other species of *Acanthochelys*, varied from small to medium in size (Ernst & Barbour 1989).

The presence of small rounded tubercles on the neck, one of the diagnostic characteristics of *A. radiolata* (Boulenger 1889; Ernst & Barbour 1989), varied considerably and the tubercles observed were either pointed, oval, very small or completely flat. Nevertheless, it is possible to differentiate the tubercles on the neck in *A. radiolata* from the tubercles in *A. spixii* and *A. pallidipectoris*, which are longer and always pointed in shape.

The carapace was the structure showing the largest morphological variation observed in this study, with part of this variation not previously reported in the literature (Mikan 1820; Gray 1844; Boulenger 1889; Ernst & Barbour 1989), such as: presence of a completely flat surface between the 2nd and 4th vertebral scutes (48.39%), rather than surface always grooved; maximum height of the carapace on the 3rd vertebral scute (78.13%) and not on the seam between 1st and 2nd vertebral scutes; lateral gutters usually formed between the 3rd and 8th marginal scutes and not only from 6th to 8th; carapacial scutes may not show growth annuli and radiating striations as frequently pointed out in the literature.

The morphological characters analyzed in the plastron also showed a variability that was not described before: median length of the intergular scute occasionally equal (36.36%) or shorter (24.24%) than its distance to the abdominals and not always longer; axillary and inguinal scutes may be present; plastral scutes may not show growth annuli and radiating striations as frequently reported in previous studies.

The variation of plastral formula observed here (Table 2) showed no correlation with sex or maturity of the specimens, although very large samples are required to exhibit all possible variations of the plastral formula (Lovich & Ernst 1989).

There are few literature records describing in detail the morphology and variation of the fore- and hindlimbs of *A. radiolata* (Mikan 1820; Duméril & Bibron 1835; Ernst & Barbour 1989). Here we first report the posterior position of the interdigital webbing relative to the claw and the presence of pointed, blunt, rounded or oval tubercles posterior to the thigh.

Luederwalt (1926) reports the presence of a greatly reduced claw on the digit V of the hindlimb, as observed here in only one specimen (MZUSP T-0062). Most species of Chelidae have 4 claws on their hindlimbs (Ernst & Barbour 1989; Bonin *et al.* 2006). Therefore, the condition observed here and in Luederwalt (1926) should be considered an abnormality.

Finally, the highest variation observed in this study was related to color pattern. Most studies of *A. radiolata* describe the carapace coloration as being dark green to brown or black (Mikan 1820; Gray 1831; Boulenger 1889; Ernst & Barbour 1989; Mocelin *et al.* 2008), although a patternless carapace was observed in only 32.35% of the specimens examined by us. Duméril & Bibron (1835) were one of the few authors who mentioned a reddish brown coloration of the carapace mixed with darker shades, which was the most frequent pattern in this study (50%).

Most literature records describe the plastron coloration as yellow with a dark or brown blotch in the middle or on each scute (Mikan 1820; Boulenger 1889; Ernst & Barbour 1989; Mocelin *et al.* 2008). This actually represents one variation of the pattern with brown streaks observed here as the most frequent coloration of the plastron (67.64%) and that was only mentioned by Bonin *et al.* (2006).

The coloration of the head, neck and limbs described here are not different from the descriptions in the literature (Mikan 1820; Gray 1831; Duméril & Bibron 1835; Ernst & Barbour 1989).

Sexual dimorphism, shape and size variation. Sexual size dimorphism in *A. radiolata* has only been documented before for the total carapace length (CL; Rhodin *et al.* 1984b). On this study, sexual size dimorphism was observed for this variable as well as nine others (Table 1). For *A. radiolata*, as well as for other chelid turtles, females attain larger sizes than males (Rhodin *et al.* 1984b; Cann 1998; Molina 1998).

The morphometric measurements of the precloacal length (PCL) and the length of the posterior plastral lobe (PLL) were performed based on Dustman (2013), who used the ratio PCL/PLL for studies on *Chelydra serpentina* and successfully demonstrated sexual differentiation, i.e., that this was a potential tool for sexing turtles.

When this ratio was used to analyze sexual dimorphism in *A. radiolata* it showed an overlapping in the amplitude of the ratio between females and males (Table 1), indicating that this method, for *A. radiolata*, is not completely accurate.

The Principal Component Analysis did not help to elucidate the size and shape variations of specimens from different geographic populations, agreeing with the high amount of polymorphism and variation that was observed in coloration and qualitative morphological characters and that is not geographically differentiated.

Ontogenetic variation. The juvenile morphology of *A. radiolata* is relatively well documented in the literature (Mikan 1820; Gray 1844; Boulenger 1889; Bonin *et al.* 2006) and for many years only the description of young specimens was known (Luederwalt 1926). Nevertheless, few studies have documented the ontogenetic variation of *A. radiolata* or compared the morphology between juveniles and adults (Bonin *et al.* 2006; Mocelin *et al.* 2008).

The most significant ontogenetic variation seen here was regarding the changes in morphology of carapace and coloration of plastron and limbs that were present when the specimens had a carapace length (CL) longer than 45 mm. This carapace length corresponds to the average CL of *A. radiolata* between the 3rd and 4th month of life documented by Mocelin *et al.* (2008). The same authors reported ontogenetic variation of color pattern of the limbs, neck and shell margins for the same stage of life, consistent with the results observed here.

In addition, the notch between the 12th marginal scutes also varied ontogenetically: it was absent in small juveniles (CL < 45 mm); present but reduced in longer juveniles (CL > 74 mm); and frequently present in subadults and adults.

Taxonomy. In a recent study on the molecular phylogeny of *Acanthochelys* using the mitochondrial genes ND4 and cyt *b* combined, Huebinger *et al.* (2013) noted that one specimen of *A. radiolata* (AK1453; unknown geographic provenance) had a high level of sequence divergence (around 4%) related to other specimens of *A. radiolata*. As this level of mtDNA divergence was equivalent to the sequence divergences among all other species of *Acanthochelys* in the study, the authors suggest that there may be additional cryptic species in this group.

Although a high level of polymorphism was observed for *A. radiolata* in this study, no clear morphological or geographic variation between populations was found that would allow us to assign the specimens into two or more distinct groups and we conclude that all specimens analyzed here represent one single species.

Acanthochelys radiolata differs from other species of *Acanthochelys* by the following combination of characters: (1) oval carapace, flat; (2) presence of a shallow longitudinal sulcus between 2nd and 4th vertebral scutes; (3) carapace and plastron scutes with radiating striations; (4) dorsal surface of the head covered with scales of irregular shape and size; (5) mesodorsal region of the head with no scales; (6) dorsal and lateral surfaces of the neck covered with small tubercles of irregular shape; (7) posterior region of the thigh with small series of tubercles (Ernst & Barbour 1989; Rhodin *et al.* 1984b; Rhodin *et al.* 2009; Vinke *et al.* 2011; this study).

Geographic distribution. Based on the specimens here analyzed, literature records (Rhodin *et al.* 1984a; Mocelin *et al.* 2008), and data from other zoological collections (MBML, MNRJ and ZUEC), we present a new geographic distribution map for the species. *Acanthochelys radiolata* is distributed in lowlands of the Atlantic forest domain at the states of Alagoas, Bahia, Espírito Santo, Rio de Janeiro and in southern Minas Gerais, these areas representing one of the biggest biodiversity hotspots of the world (Myers *et al.* 2000).

Here we do not confirm the presence of this species at São Paulo and Mato Grosso states. The record of *A.*

radiolata from the city of São Sebastião, state of São Paulo, was misinterpreted by Rhodin *et al.* (1984a), who referred to the type locality of the species as "Sebastianopolis" (Mikan 1820). Later, Iverson (1992) indicated that actually "Sebastianopolis" refers to the old name of the city of Rio de Janeiro, at the state of the same name. Although this correction was effected more than 20 years ago, the record of *A. radiolata* from São Paulo state persisted in the literature (Fritz & Havaš 2007; TTWG 2011, 2014), even though the species was not reconfirmed from there by subsequent workers.

The two voucher specimens (MNRJ 2466 and MNRJ 2467) from the Culuene River, municipality of Jacaré, Mato Grosso state, were first mentioned by Rhodin *et al.* (1984a). One of the specimens was analyzed in this study and proved to represent *A. radiolata* (identification by R.C.G) although this record is outside of the core geographic distribution of the species.

These two adult females were catalogued as being collected by G. Myers and A. L. de Carvalho on June 1950 in addition to two other turtles, *Podocnemis unifilis* (MNRJ 2463) and *Phrynops geoffroanus* (MNRJ 2464), which indeed are present in Mato Grosso state. However, Myers & Carvalho (1959), when describing a new characid fish from the Culuene River, stated that only Mr. Carvalho collected this specimen in June 1950 and that Mr. Myers did not go to that expedition. The catalogue entry for the turtles is therefore dubious.

It is known that G. Myers was assigned by the United States Fish Department to work in Brazil between 1942 and 1944, where he was conducting both curatorial and research activities in ichthyology at the Museu Nacional (Weitzman & Menezes, 1989). There he met A. L. Carvalho, at the time curator in Herpetology, and together they undertook many expeditions in Southeast Brazil and collected both ichthyological and herpetological material (Nomura, 1993).

Also, A. L. de Carvalho used to keep and breed turtles at his home in Rio de Janeiro (Ulisses Caramaschi, pers. comm.). It seems very likely that the *A. radiolata*, *P. unifilis* and *Ph. geoffroanus* specimens were collected during different expeditions, that the original geographic locality data was lost or that these animals were from the curator's private collection and were mixed during the cataloguing process.

Over the last 60 years, the upper Xingu River basin has been explored by scientists and field workers, both zoologists and archeologists (Heckenberger *et al.* 2007, Zawadzki *et al.* 2008, Moreira *et al.* 2011) and *A. radiolata* has never again been found in Mato Grosso or in the area nearby. This would not be the first record of curatorial mistakes and wrongly assigned localities in the history of turtle taxonomy (Stuckas *et al*. 2013). Thus, we strongly suggest that the locality recorded for *A. radiolata* in Mato Grosso state should not be considered a valid locality for the distribution of the species.

Conclusion

Morphological analysis revealed that *A. radiolata* is a polymorphic turtle species, regarding mainly color and shape variation. This species may present two basic color variations for the carapace and three for the plastron. *Acanthochelys radiolata* shows significant results for sexual size dimorphism for nine morphometric variables, including carapace length, and the females reach larger sizes than males. Carapace morphology and coloration of limbs change during different life stages for juveniles of *A. radiolata*.

Acanthochelys radiolata is distributed in Brazil in the Atlantic forest domain of the states of Alagoas, Bahia, Espírito Santo, Rio de Janeiro and in southern Minas Gerais, but the previous records in Mato Grosso state seems questionable.

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APPENDIX 1. Specimens examined.

COUNTRY: **State:** Municipality, Locality: specimen

Legend: * dry specimens; # not included in the morphometric analysis; [1] included only in statistical analysis; [2] syntypes of *Platemys radiolata quadrisquamosa*.

Acanthochelys radiolata (n =41): BRAZIL: **Alagoas:** Passo de Camaragibe, Fz. Morro de Camaragibe: MZUSP T.4362; **Bahia:** Belmonte: MZUSP T.337*2; Trancoso: MNRJ 19625; Porto Seguro, 15km NW, CEPLAC, Estação Ecológica Pau Brasil: MZUSP T.3094; Mucuri: ZUEC 1434; **Espírito Santo:** Guarapari, P.E. Paulo César Vinha, Lagoa Feia: MNRJ 20055; Linhares: MNRJ 3809, 3810, MZUSP T.2696, Reserva Florestal da CVRD: ZUEC 1833*; Vitória, arredores do P.E. da Fonte Grande: MNRJ 18520*; Rio Doce: MZUSP T.062*2, T.064*2; Santa Teresa, Escola Prática de Agricultura: MNRJ 10521, 1053, 1054, 1055, 1056, 10581, 1059; **Mato Grosso:** Jacaré, rio Culuene: MNRJ 2466; **Minas Gerais:** Muriaé: MZUSP T.3035; **Rio de Janeiro:** Arraial do Cabo: MNRJ 7282; Itaboraí: MZUSP T.4373; Macaé, Terminal Cabiúnas: MNRJ 20068, 20069, Ilha de Santana: MNRJ 7280#; Maricá, Lagoa de Maricá: MNRJ 8699; Niterói: MNRJ 3812, São Francisco: MNRJ 3792#; Rio de Janeiro: MNRJ 3808, 7308, NMW 23390, Jacarepaguá: MNRJ 24151, Recreio dos Bandeirantes: MNRJ 1050, 2485, 2486, Jardim Botânico do Rio de Janeiro, Lago maior: MNRJ 19822; São

João da Barra: Grussaí: MNRJ 24881, 2489, 24901.

Acanthochelys macrocephala (n = 2): BRAZIL: **Mato Grosso**: São Luis de Cáceres, rio Paraguai: MNRJ 1065; **Mato Grosso do Sul**: Aquidauana: MZUSP T.3168.

Acanthochelys pallidipectoris (n = 1): ARGENTINA: **Salta**: Anta, camino entre Santo Domingo e Los Colorados: MZUSP 1068.

Acanthochelys spixii (n = 5): BRAZIL: **Distrito Federal**: Brasília: MNRJ 3814; **Minas Gerais**: Lagoa Santa: MNRJ 1397, 1398; Serra da Canastra: MZUFV 048; **São Paulo**: Piraju: MNRJ 3813.

Supporting information

The following Supporting Information is available for this article:

APPENDIX S1. List of the morphological and morphometric characters used in this study, references and abbreviations (when applicable).

CHARACTER	REFERENCE	ABB
Morphometrics		
Head length	Mikan, 1820	HL
Head width	Mikan, 1820	HW
Interorbital minimum width	Modified from McCord, Joseph-Ouni and Lamar, 2001	IOW
Carapace maximum linear length	Mikan, 1820	CL
Carapace median length	This Study	CML
Carapace maximum width	Ernst, 1983	CW
Carapace width at anterior margin	Modified from Mikan, 1820	CWA
Carapace width at posterior margin	Modified from Mikan, 1820	CWP
Carapace height at the suture between 2nd and 3rd vertebral scutes	Ernst, 1983	CH
Cervical scute maximum length	This Study	CVL
4th vertebral scute maximum length	Ernst, 1983	4VL
3rd pleural scute maximum length	This Study	3PL
Plastron maximum length	Ernst, 1983	PL
Plastron median length	McCord, Joseph-Ouni and Lamar, 2001	PML
Plastron maximum width	Mikan, 1820	PW
Plastron maximum width with the bridge	This Study	PWB
Plastron posterior lobe length	Dustman, 2013	PLL
Intergular scute median length	Lovich and Ernst, 1989	Interg
Gular maximum length	Lovich and Ernst, 1989	Gul
Interhumeral seam length	Lovich and Ernst, 1989	Hum
Interpectoral seam length	Lovich and Ernst, 1989	Pect
Interabdominal seam length	Lovich and Ernst, 1989	Abd
Interfemoral seam length	Lovich and Ernst, 1989	Fem
Interanal seam length	Lovich and Ernst, 1989	Anal
Bridge maximum length	Ernst, 1983	BL
Bridge maximum width	This Study	BW
Precloacal length	Dustman, 2013	PCL
Precloacal length/Plastron posterior lobe length	Dustman, 2013	PCL/PLL

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APPENDIX S1. (Continued)

CHARACTER	REFERENCE	ABB
Quantitative morphological		
Number of post-orbital scales	Ernst, 1983	
Number of post-nasal scales	This Study	
Number of tympanum-orbit scales	Modified from Ernst, 1983	
Number of barbels	Ernst and Barbour, 1989	
Number of marginal scutes	Mikan, 1820	
Number of forelimb lateral scales (in line)	This Study	
Number of forelimb flap lateral scales	This Study	
Number of forelimb fist scales (in line)	This Study	
Number of hindlimb lateral scales (in line)	This Study	
Number of hindlimb flap lateral scales	This Study	
Number of post-hindlimb tubercles (in transversal line)	This Study	
Number of dorsal scales on digit I of hindlimb	Luederwalt, 1926	
Qualitative morphological		
Shape of the head	Mikan, 1820	
Dorsal shape of the head	Mikan, 1820	
Scales on the head	Mikan, 1820	
Position of the scales on the head	This Study	
Central tegument of the head	This Study	
Snout shape in dorsal view	Mikan, 1820	
Snout shape in lateral view	This Study	
Size of the snout related to the size head	Mikan, 1820	
Upper jaw notch	Ernst and Barbour, 1989	
Relation between posterior end of upper jaw and the anterior end of the orbit	This Study	
Excrescence of skin at the posterior end of the mouth	This Study	
Position of the eyes on the head	Mikan, 1820	
Size of the barbels related to the size of the head	Ernst and Barbour, 1989	
Scales on the neck	This Study	
Position of the scales on the neck	This Study	
Dorsal tubercles on the neck	Mikan, 1820	
Shape of the dorsal tubercles on the neck	Mikan, 1820	
Lateral tubercles on the neck	Ernst and Barbour, 1989	
Shape of the lateral tubercles on the neck	This Study	
Size of the lateral tubercles on the neck	Ernst and Barbour, 1989	
Dorsal tubercles at the posterior region of the neck	Bonin, Devaux and Dupré, 2006	
Shape of the carapace	Mikan, 1820	
Dorsal shape of the carapace	Mikan, 1820	
Lateral gutters on the carapace	Bonin, Devaux and Dupré, 2006	
Vertebral scute where the carapace is higher	Ernst and Barbour, 1989	
Marginal scute where the carapace is wider	Ernst and Barbour, 1989	

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APPENDIX S1. (Continued)

CHARACTER	REFERENCE	ABB
Shape of the anterior margin of the carapace	Mikan, 1820	
Longitudinal sulcus between 2nd and 4th vertebral scutes	Mikan, 1820	
Relation between length and width of the cervical scute	This Study	
Growth annuli on carapacial scutes	This Study	
Radiating striations on carapacial scutes	This Study	
Growth annuli on ventral surface of marginal scutes	This Study	
Radiating striations on ventral surface of marginal scutes	This Study	
Length of the anterior margin of the plastron related to the carapace	This Study	
Length of the posterior margin of the plastron related to the carapace	This Study	
Growth annuli on plastral scutes	This Study	
Radiating striations on plastral scutes	This Study	
Anal notch	Bonin, Devaux and Dupré, 2006	
Marginal scute in contact with pectoral-abdominal suture	McCord, 2007	
Marginal scutes in contact with pectoral scutes	This Study	
Marginal scutes in contact with abdominal scutes	This Study	
Relation between length and width of the intergular scute	This Study	
Relation between length and width of the pectoral scute	This Study	
Relation between length and width of the abdominal scute	This Study	
Contact between gular scutes	This Study	
Contact between humeral scutes	This Study	
Median length of intergular scute related to the distance between intergular and abdominal scute	Ernst and Barbour, 1989	
Width of the anterior plastron lobe related to the width of posterior plastron lobe	Ernst and Barbour, 1989	
Plastral formula	Ernst and Barbour, 1989	
Axillary scute	This Study	
Inguinal scute	This Study	
Interdigital webbing length related to the level of claw insertion (forelimb)	Mikan, 1820	
Scales on the lateral surface of the forelimb	Ernst and Barbour, 1989	
Size of the scales on the lateral surface of the forelimb	Ernst and Barbour, 1989	
Scales on the medial surface of the forelimb	This Study	
Size of the scales on the medial surface of the forelimb	This Study	
Number of digits on the hindlimb	Mikan, 1820	
Claw on digit V of the hindlimb	This Study	
Interdigital webbing length related to the level of claw insertion (hindlimb)	Mikan, 1820	
Scales on the lateral surface of the hindlimb	Ernst and Barbour, 1989	
Size of the scales on the lateral surface of the hindlimb	Ernst and Barbour, 1989	
Scales on the medial surface of the hindlimb	This Study	
Size of the scales on the medial surface of the hindlimb	This Study	
Posterior tubercles on the thigh	Ernst and Barbour, 1989	

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APPENDIX S1. (Continued)

CHARACTER	REFERENCE	ABB
Shape of the tubercles on the thigh	Ernst and Barbour, 1989	
Size of the tubercles on the thigh	This Study	
Coloration		
Dorsal coloration of the head	Mikan, 1820	
Ventral coloration of the head	Mikan, 1820	
Coloration of the upper jaw	Ernst and Barbour, 1989	
Coloration of the lower jaw	Ernst and Barbour, 1989	
Dorsal coloration of the neck	Mikan, 1820	
Ventral coloration of the neck	Mikan, 1820	
Coloration pattern of the carapace	Mikan, 1820	
Coloration pattern of the plastron	Mikan, 1820	
Coloration of the lateral surface of the forelimb	Mikan, 1820	
Coloration of the medial surface of the forelimb	Mikan, 1820	
Coloration of the lateral surface of the hindlimb	Mikan, 1820	
Coloration of the medial surface of the hindlimb	Mikan, 1820	

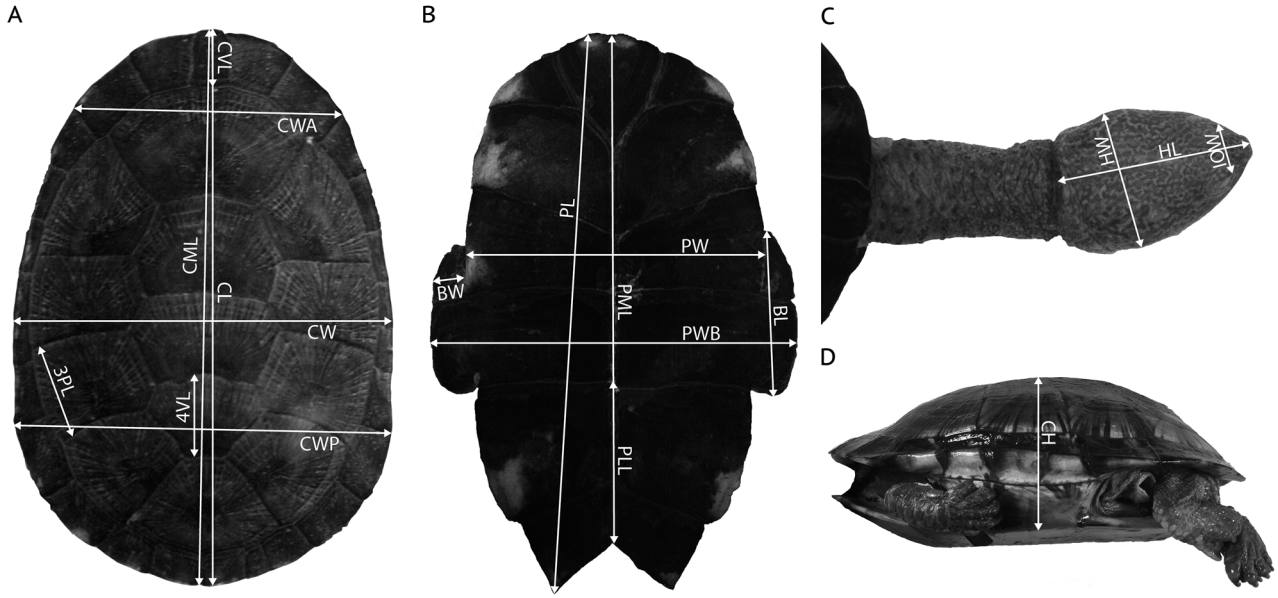

FIGURE S1. Morphometric characters taken at the (**A**) carapace, (**B**) plastron, (**C**) head, and (**D**) lateral of the shell. **A**: Carapace maximum length (CL); Carapace median length (CML); Carapace maximum width (CW); Carapace width at anterior rim (CWA); Carapace width at posterior rim (CWP); Cervical scute maximum length (CVL); 4th vertebral scute maximum length (4VL); 3rd pleural scute maximum length (3PL). **B:** Plastron maximum length (PL); Plastron median length (PML); Plastron maximum width (PW); Plastron maximum width with the bridge (PWB); Plastron posterior lobe length (PLL); Bridge maximum length (BL); Bridge maximum width (BW). **C:** Head length (HL); Head width (HW); Interorbital minimum width (IOW). **D:** Carapace height at the suture between 2nd and 3rd vertebral scutes (CH).